

THE GENUS GYMNOCLADUS AND ITS TROPICAL AFFINITY

YIN-TSE LEE

THE CAESALPINIOIDEAE is generally regarded as a predominantly tropical subfamily of the Leguminosae. On the basis of a preliminary survey of some 180 genera listed by Heywood (1971), I am able to show (unpublished data) that about 79 (44.38 per cent)¹ are endemic to tropical Africa as compared to 44 (24.72 per cent) in tropical America and 26 (14.62 per cent) in tropical Asia. The abundance of endemic genera in tropical Africa indicates that this area may be the center of diversity for the subfamily. This view is well supported by a series of studies carried out by Léonard (1950, 1951, 1957), Hutchinson and Dalziel (1958), and Brenan (1965, 1967). On the other hand, tropical America, especially the Amazon Basin, has been suggested by Ducke and Black (1955; see also Langenheim, Lee, & Martin, 1973) as a secondary center of diversity for the subfamily Caesalpinioideae. The phytogeographical significance of the Asiatic Caesalpinioideae, however, has long been overlooked. With the 26 endemic genera occurring in tropical Asia, and the apparent affinity of these Asiatic representatives to African ones (12 genera are found exclusively in tropical Asia and Africa, the so-called Old World Tropics, in contrast to only two genera of this subfamily represented in both Asia and America), a comprehensive study of the Asiatic genera is not only desirable, but also necessary for an understanding of the evolutionary history of the subfamily.

Among the Asiatic genera, the Chinese taxa are of particular interest, as there are about 17 genera and some 80 species of Caesalpinioideae, representing a wide spectrum of diversity in their distributional pattern. For example, the monotypic genera *Lysidice* and *Zenia* are known only in tropical and subtropical China. *Erythrophleum*, *Cynometra*, *Saraca*, *Sindora*, *Intsia*, *Mezoneuron*,² *Pterolobium*, *Peltophorum*, and *Parkinsonia* are represented in tropical China by one or two species with much restricted distribution, whereas *Cercis*, *Gleditsia*, *Gymnocladus*, *Caesalpinia*, and occasionally several annual *Cassia* species have a much wider distribution, extending into the warm temperate regions as well (TABLE 1).

Since very little has been written in western literature about the Chinese tropical area and its phytogeographical significance, a brief review of the Chinese tropics and a summary of some of the more recent considerations of floristic affinities of the Chinese tropical areas to other parts of the world are given here.

The tropical area of China is restricted to a narrow zone along the southern border. It starts in southeastern Yunnan and extends eastward

¹Brenan (1965) in a study of 81 genera of Caesalpinioideae listed 54, i.e. 66.66 per cent, as endemic to tropical Africa.

²Vidal and Thol (1974) consider *Mezoneuron* to be a subgenus of *Caesalpinia*.

TABLE 1. Chinese genera of the Caesalpinioideae.*

	NO. OF SPECIES IN CHINA	DISTRIBUTION	REMARKS
Dimorphandreae			
<i>Erythrophleum</i>	1	Chekiang, Fukien, Kwangtung, Taiwan	
Caesalpinieae			
<i>Caesalpinia</i>	ca. 18	Shensi, Kiangsu, Anhwei, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Taiwan, Kwangtung, Kwangsi, Kweichow, Szechwan, Yunnan	
<i>Gleditsia</i>	7	Widely distributed in N.E., E., Central, S., & S.W. China	
<i>Gymnocladus</i>	2	Kiangsu, Anhwei, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Kwangtung, Kwangsi, Szechwan, Yunnan	
<i>Mezoneuron</i>	1	Yunnan, Kwangtung (Hainan)	
<i>Parkinsonia</i>	1	Kwangtung (Hainan)	Introduced?
<i>Peltophorum</i>	1	Kwangtung (Hainan)	
<i>Pterolobium</i>	1-2	Hupeh, Szechwan, Yunnan, Hu- nan, Kwangtung, Kwangsi	
Cassieae			
<i>Cassia</i>	ca. 13	N.E. China, Shantung, Hopeh, Fukien, Kwangtung, Kwangsi, Yunnan, Taiwan	
<i>Zenia</i>	1	Hunan, Kwangtung, Kwangsi, Kweichow, Yunnan	Endemic
Detarieae			
(Cynometreae)			
<i>Cynometra</i>	1	Kwangtung (Hainan)	
<i>Intsia</i>	1	Taiwan	
<i>Lysidice</i>	1	Kwangtung, Kwangsi, Kweichow, Yunnan, Taiwan	Endemic
<i>Saraca</i>	1-2	Kwangtung, Kwangsi, Yunnan	
<i>Sindora</i>	1	Kwangtung (Hainan)	
Cercieae			
(Bauhinieae)			
<i>Bauhinia</i>	ca. 25	Kansu, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Kwangtung, Kwangsi, Kweichow, Szechwan, Yunnan, Taiwan	
<i>Cercis</i>	6	Anhwei, Hupeh, Szechwan, Kweichow, Kwangtung, Kwangsi, Yunnan, Kansu, Liaoning, Shensi	

* Genera are arranged alphabetically by tribes. Tribal designation is according to that of Heywood (1971). Tribes without representatives in China are excluded.

via Kwangsi to the coastal provinces of Kwangtung and Fukien, including the offshore islands of Taiwan and Hainan, as well as the South Sea Islands. The boundary and even the existence of the Chinese tropics were subjects of controversial argument that stirred up considerable interest in several Chinese journals in the 1950's and early 1960's (see Chin, 1956; Yen, 1961; Young, 1961; Lou, Feng, & Chiu, 1961). In a brief review, Tsang (1964) pointed out that the confusion was due mainly to the use of different terminologies. He further concluded that although there is only a small equatorial tropical zone in China, a considerable area which may be classified as tropical is present. According to his scheme, the Chinese tropics are composed of two parts, the equatorial tropical zone and the tropical zone. The former may be subdivided into the equatorial zone and the equatorial monsoon zone, whereas the latter may be subdivided into the tropical monsoon zone and a transitional zone. On a regional basis, six districts are recognized: (1) the tropical mountainous area of southern Yunnan, (2) the limestone mountains of Kwangsi, (3) Hainan, (4) the highland along Kwangtung and Fukien, (5) Taiwan, and (6) the South Sea Islands (FIGURE 1). In spite of the regional differences, which are subject to various local factors, the floristic elements in these areas indicate a close relationship to the India-Burma flora, with the exception of those in Taiwan and probably the South Sea Islands, which show an affinity to the flora of the Philippines.

Evidence derived from floristic composition also supports the existence of a tropical flora in China. Members of the Annonaceae, Moraceae, Connaraceae, Flacourtiaceae, and Passifloraceae are very abundant in southern Yunnan and in Hainan (see Wu, 1965; Wu & Wang, 1957-1958; Wu & Li, 1965; Fedorov, 1958). Woody epiphytes, characteristic of tropical rain forests, are also abundant in the areas cited (Fedorov, 1959). According to Fedorov (1959), the rarity of members of the Dipterocarpaceae (represented by three species of *Hopea* and one species of *Vatica*) is due to historico-floristic factors rather than to climatic influence.

In a systematic survey of the Chinese caesalpinioaceous plants, *Gymnocladus* is chosen here for a more detailed study because it is a small genus composed of only four species and because it is the only genus of the Caesalpinioideae confined to eastern North America and eastern Asia. Although *Gymnocladus* is generally regarded as a genus of temperate areas, the presence of *G. burmanicus* and *G. assamicus* in the mountains of the tropical zone may indicate a strong tropical affinity for the genus. *Gymnocladus* has a rich fossil record, which, when combined with other information (e.g., that concerning the Tertiary climate and the present distribution of the genus), will facilitate interpretation of migration routes of the genus in the past.

TAXONOMIC HISTORY

The genus *Gymnocladus* was established in 1785 by Lamarck, in reference to the "naked branches" of the trees in winter. Lamarck cited two

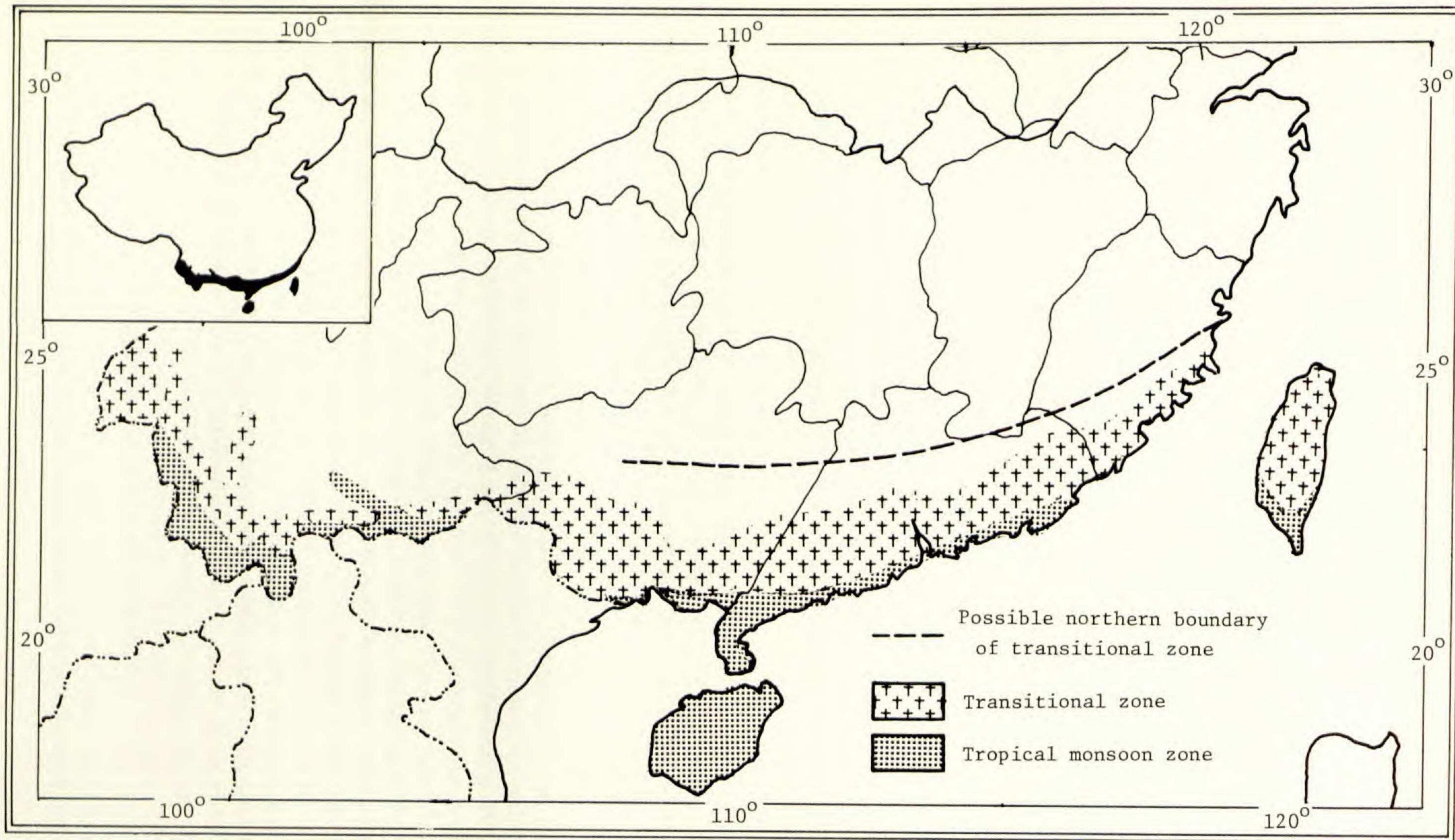


FIGURE 1. Tropical zones of China (according to Tsang, 1964, with minor modifications). Insert showing relative position of the Chinese tropical zones.

species under the genus, *G. canadensis* from eastern Canada and *G. arabicus* from Egypt. The plant which Lamarck called *G. canadensis* was known by some earlier botanists. It was mentioned by Linnaeus (1742, 1753) as *Guilandina dioica*. Duhamel (1755) described and illustrated the plant under the generic name "Bonduc" in his *Traité des Arbres*. Vahl (1790) referred both *Guilandina dioica* and *Gymnocladus canadensis* to his *Hyperanthera dioica*. It was not until 1869 that Koch transferred *Guilandina dioica* to *Gymnocladus* and recognized it as an earlier name for *Gymnocladus canadensis*. On the other hand, *Gymnocladus arabicus*, the second species of the genus described by Lamarck, is now considered to be synonymous with *Moringa aptera* of the Moringaceae. Baillon (1875) described *G. chinensis* from "Shanghai," China. *Gymnocladus Williamsii*, described from Peking, China (Hance, 1884), has been placed in synonymy with *Gleditsia sinensis* Lam. Two other species, *Gymnocladus burmanicus* and *G. assamicus*, have been described from Burma (Parkinson, 1928) and Assam, India (Kanjilal, 1934) respectively.

MORPHOLOGICAL CHARACTERS

HABIT. Deciduous trees from 6 to 20 meters tall. Bark silver-gray, occasionally tinged with red, deeply fissured or not; the pith of young branches purplish.

LEAVES. Leaves bipinnate, occasionally pinnate; stipules lanceolate or slightly obovate; petioles abruptly and conspicuously enlarged at the base, with 3-7 pairs of subopposite to opposite pinnae; leaflets in each pinna varying in number according to species, ovate, oblong to oblanceolate, entire, the apex acuminate to rounded, mucronate, the base cuneate to rounded, slightly oblique, the petiolules 2-4 mm. long, the midrib prominent only on the abaxial surface, with 6-8 pairs of secondary veins joined together in a series of arches (brochidodromous, FIGURE 3), the stipels small, awl-shaped, and persistent or absent.

INFLORESCENCE AND FLOWERS. Inflorescence racemose to occasionally paniculate, erect to pendulous, usually appearing with the new leaves, the branches and pedicels hoary-tomentose, usually longer in those with "perfect" flowers than in those with only staminate flowers. Staminate flowers characterized by a rather narrow floral tube, with 10 fertile stamens, rudimentary pistil usually present. In the morphologically bisexual flowers, the pistil is well-developed, whereas the majority of stamens are characterized by having poorly developed anthers with pollen absent or apparently abortive. Thus, most of the apparently bisexual flowers are, in fact, functionally unisexual. This phenomenon has been described as dioecism by abortion (see Sargent, 1892). Calyx tubular, with 10 longitudinal veins, the lobes 5-4, greenish, lanceolate, valvate, and not fully enclosing the petals within; petals 5-4, greenish to creamy white, occasionally purplish on the adaxial surface, imbricate in bud; stamens in

2 whorls, 5 long alternating with 5 short, inserted on the margin of the floral tube, the anthers uniform, orange or yellowish, all fertile or abortive, the filaments pilose near the base; pistil sessile to subsessile, covered with thin pilosity throughout, rudimentary or lacking in staminate flowers, the style short, erect, obliquely dilated or slightly capitate, ovules 4 to many. Pollen grains tricolporate, ellipsoid-oblong, the exine perforate-tectate, reticulate (FIGURE 2).

FRUIT. Oblong to falcate, turgid to compressed, woody to subwoody, smooth or ridged and grooved, dark brown, usually covered with a glaucous bloom, with endocarp pulpy (greenish and slimy when fresh), dehiscent along the placental suture when mature.

SEEDS. One to several, ovoid to subglobose, surrounded by the endocarpic pulp; funicle stout, ca. 5 mm. long; testa bony, dark brown; embryo straight, surrounded by a copious, cartilaginous endosperm, the cotyledons ovate, thick, and fleshy, the radicle short, erect.

SEEDLINGS. Germination of seeds hypogeous (at least in *G. dioicus*; see U.S.D.A., 1948); juvenile leaves once-pinnate.

GENERIC RELATIONSHIPS

The genus *Gymnocladus* was originally assigned to tribe Cassieae by De Candolle (1825a, b) under his suborder Caesalpinioideae of the family Leguminosae. It was later transferred to tribe Caesalpinieae (as Eucaesalpinieae) by Bentham (1840). Bentham's tribal classifications of the Caesalpinioideae have been accepted by many later workers. Hutchinson (1964), however, was dismayed by the seemingly minor and occasionally overlapping characters employed by Bentham in delimiting the tribes, and he reclassified the subfamily, relying heavily on the foliar characters. As a result, Hutchinson assigned most of the genera in the Caesalpinieae and Dimorphandreae (both *sensu* Bentham) to Group V of the Caesalpinioideae.³

In a recent summary Heywood (1971) listed 27 genera under tribe Caesalpinieae. My discussion here, however, will be limited to the relationship between *Gymnocladus* and *Gleditsia* for the following reasons. First, as indicated by Bentham (1866), both genera have polygamous flowers, with the calyx lobes not completely covering all the petals in the bud and some of the petals therefore almost having the appearance of sepals. This represents a very unusual (if not unique) condition in the Leguminosae. Secondly, *Gymnocladus* is usually placed close to *Gleditsia* in various taxonomic works (see De Candolle, 1825a, b; Bentham & Hooker, 1865; Taubert, 1891; Burkart, 1952), suggesting their close relationship.

³ Hutchinson recognized five groups in the Caesalpinioideae, which together with his *Brachystegioideae* comprise the Caesalpinieae.

Gymnocladus and *Gleditsia* share many characters in common. Some of the striking similarities are the nature of the calyx, as mentioned by Bentham (1866), and the presence of the so-called polygamous flowers. Polygamy, when used without any clarification, is a rather confusing term. It has been defined as the condition of having staminate, carpellate, and hermaphrodite flowers on the same individual (Henderson & Henderson, 1963). The relative proportion of the three kinds of flower, however, may vary even among individuals within the same population. In the flowers of *Gymnocladus* and *Gleditsia*, usually only one type of reproductive organ is functional, although a rudimentary or abortive organ of the opposite sex may be present. This phenomenon may be interpreted as incomplete dioecism.

The morphological differences between the staminate and carpellate ("perfect") flowers and inflorescences in the various species of *Gymnocladus* are rather slight compared with the differences in the species of *Gleditsia*; the tendency toward dioecism is much greater in *Gleditsia* than in *Gymnocladus*. In *Gleditsia*, the staminate flowers are significantly different from the morphologically bisexual (but functionally carpellate) flowers. Although true polygamy has been reported for *G. triacanthos* in the literature (O'Rourke, 1949; Grisiuk, 1952), individual trees are characterized, for the most part, by their having only one kind of flower. *Gleditsia* should therefore be considered as a predominantly dioecious genus (Lee, unpublished manuscript). Further supporting evidence may be derived from the differentiation of two kinds of inflorescence which accompany the evolution of unisexual flowers in most species of the genus. The staminate inflorescence is spikelike, characterized by many small and highly congested flowers, whereas the carpellate ("perfect") inflorescence is a lax raceme with larger and many fewer flowers.

The seeds of *Gymnocladus* and *Gleditsia* are smooth, with hard testa and large amounts of cartilaginous endosperm surrounding the embryo. The endosperm consists of thick-walled cells, which upon the addition of water are converted into "mucilage" (see Pammel, 1899; Sayed & Beal, 1958). The presence of such endosperm suggests the close relationship of the two genera, although similar endosperm has also been found in some species of *Cercis*, *Hoffmannseggia* (Pammel, 1899), *Bauhinia*, and *Erythrophleum* (see Corner, 1951). The presence of copious endosperm is generally regarded to be a primitive character. This coincides with the seemingly undifferentiated flowers of *Gymnocladus* and *Gleditsia*, but it is in contrast to the occurrence of dioecism.

Gymnocladus and *Gleditsia* are known to lack nodule formation in their roots (see Allen & Allen, 1936), a character considered by Burkart (1952) to be "primitive." In a review of nodulation among leguminous plants, Allen and Allen (1961) indicated that only about 24 per cent of the 115 species (which represent 40 genera) form nodules. This percentage is significantly low when compared with percentages in the Mimosoideae and Faboideae (87 per cent in 146 species of 21 genera and 94 per cent in 1024 species of 182 genera respectively). In a recent study

of nodulation among Rhodesian leguminous plants, Corby (1974) revealed a similar low percentage of nodulation among members of the Caesalpinioideae. Thus, the lack of nodule formation should be regarded as significant at the subfamily level only. It may be the result of the tropical environment and the arboreal nature usually associated with the subfamily.

The two genera are also known for their richness in saponins. In fact, fruits of *Gymnocladus chinensis* and several species of *Gleditsia* are commonly used in China as soap substitutes. In this study an attempt has been made to use this character of the chemical constituents as an aid in classification. On the basis of a preliminary investigation of fruit saponins in the two genera, the aglycones (which together with various sugars are the products of hydrolysis of saponins) are found to be triterpenoid in nature (Parkhurst & Lee, unpublished data). Of the three species of *Gleditsia* (*G. triacanthos*, *G. sinensis*, and *G. officinalis*) and the three species of *Gymnocladus* (*G. dioicus*, *G. chinensis*, and *G. assamicus*) studied, a distinct set of aglycones was observed for each genus, although the quantity of each component varied in different species. Among the three *Gleditsia* species there are eight major components, with oleanolic acid as the predominant compound, whereas among the *Gymnocladus* species four major compounds are present. The triterpenoid aglycones found in *Gleditsia* are either lacking or significantly small in quantity in *Gymnocladus*, and *vice versa*. In other words, chemical characters (saponin chemistry) may be used to separate the two genera, but they have little value in delimiting various species of the same genus. This finding nevertheless indicates the homogeneity within each of the genera. The presence of structurally similar triterpenoid saponins in the two genera furthermore suggests a close affinity.

On the basis of the morphological characters (particularly the less differentiated flowers) and the nature of dehiscence of the fruit, it seems reasonable to conclude that in the tribe Caesalpinieae, *Gymnocladus* represents a more "primitive" genus than *Gleditsia*. This contrasts with the phylogenetic arrangement generally inferred (see Taubert, 1891; Burkart, 1952). However, this arrangement does not indicate that *Gleditsia* is derived from *Gymnocladus*.

Gymnocladus can be easily separated from *Gleditsia* by the nature of the fruit, which is dehiscent along the placental suture; by the erect, racemose inflorescence and the larger flowers; by the absence of spines on the trunk and branches; by the presence of small, awl-shaped, persistent stipels (Asiatic species only); and by the presence of triterpenoid aglycones with higher molecular weight. Other similarities and differences are listed in TABLE 2.

DISCUSSION

Of the four *Gymnocladus* species, *G. chinensis* and *G. dioicus* have disjunct distributions in the vast temperate areas of eastern China and the

eastern United States respectively. For this reason *Gymnocladus* has long been regarded as a genus of temperate regions. The two more recently described species, *G. burmanicus* and *G. assamicus*, have been overlooked in the literature. It is of particular interest that both of these species have a very restricted distribution, being found exclusively in the mountainous areas of the tropical zone of Asia. The species thus serve as

TABLE 2. Comparison of *Gymnocladus* and *Gleditsia*.

	Gymnocladus	Gleditsia
HABIT	Trees	Trees to shrubs
SPINES	Absent	Simple or compound
LEAVES	Bipinnate, rarely pinnate	Pinnate to bipinnate
EPIDERMIS	Margins sinuous	Margins straight
VENATION OF LEAFLETS	Brochidodromous	Craspedodromous to brochidodromous
FLOWERS	Predominantly dioecious	Predominantly dioecious
FLORAL TUBE	Tubular, elongated, hoary-pubescent	Short, turbinate, glabrate or pubescent
POLLEN	Tricolporate, exine reticulate	Tricolporate, exine reticulate
FRUIT	Oblong to falcate, dehiscent along placental suture	Oval to elongate, indehiscent to tardily dehiscent
PULP	Present	Present or not
TRITERPENOID SAPONINS	Present	Present
SEEDS	Large (ca. $1.5 \times 1.5 \times 1$ cm.), subglobose	Small (ca. $1-1.5 \times 0.5-0.8 \times 0.3-0.5$ cm.), subquadrate to obovoid
ENDOSPERM	Copious and cartilaginous	Copious and cartilaginous
GERMINATION	Hypogeal, juvenile leaves pinnate	Epigeal, juvenile leaves pinnate
CHROMOSOME NUMBER	$2n = 28$	$2n = 28$
NUMBER OF SPECIES	ca. 15	4
EXTANT GEOGRAPHICAL DISTRIBUTION	E. North America, E. & S.E. Asia, Burma and N.E. India	E. North America, Central South America, E. Asia extending to Malaya
REPORTED FOSSIL RECORDS	E. & W. North America, E. Asia, and Europe	E. & W. North America, E. Asia, and Europe

good indications of a tropical origin of the genus. A possible tropical origin of *Gymnocladus* is also supported by the overall tropical affinity of members of the subfamily Caesalpinioideae. Further evidence supporting such an origin of *Gymnocladus* may be derived from the floral structure of the genus. The predominantly dioecious flowers⁴ of *Gymnocladus*, as exemplified by those of *G. dioicus*, are relatively large (flowering buds immediately before anthesis measured up to 1.8 cm. in length from the apices of the calyx lobes to the base of the floral tube, and 0.4–0.6 cm. in diameter at the widest part); are borne on a rather long and showy raceme or panicle; have a strong scent; bear abundant nectar within the floral tube; are frequently visited by small insects; and are characterized by the presence of an abortive/rudimentary organ of the opposite sex in both the staminate and carpellate flowers. All of these characteristics agree with the “syndromes” of the dioecious tree taxa in the tropics described by Bawa and Opler (1975) and contrast sharply with the usually very small, highly reduced, and predominantly wind-pollinated dioecious plants typical of temperate regions (e.g., the Amentiferae).

Furthermore, contemporary thinking in paleobotany indicates that plants regarded as “temperate” had broader and less definite ecological requirements, with their total geographical ranges larger than generally recognized, and they may have been associated with rather different ecotypes during various segments of their geographical history (Graham, 1972). This viewpoint again supports a possible tropical origin of the genus *Gymnocladus*. A similar situation may exist in a number of “temperate” genera, such as *Fagus*, *Liriodendron*, *Tilia*, *Nyssa*, and *Myrica*, which are also found in tropical or subtropical communities today.

The bicentric distribution of *Gymnocladus*, on the other hand, is part of the more elaborate distributional pattern known as the Tertiary relict disjunction, since fossil remains attributed to this genus have also been found in Europe and western North America. The long known eastern Asiatic–eastern North American floristic relationships have been discussed extensively in the past (see Gray, 1840, 1846; Fernald, 1929; Li, 1952; Graham, 1972; Wood, 1972) and will not be considered further here. However, with the discovery of two highly restricted species of *Gymnocladus*, *G. burmanicus* and *G. assamicus*, the “boundary” of eastern Asia becomes extended westward to include Assam and southern Yunnan, and southward to include Lower Burma. The presence of these two species of *Gymnocladus* in the mountainous regions of the tropical zone is of great phytogeographical significance, as they may be the remnant species of a once more widespread tropical stock.

In discussing ecological evolution of flowering plants and the origin of the temperate flora, Takhtajan (1969) suggested that angiosperms

⁴Dioecism is a rarity in the Caesalpinioideae. Other than in *Gymnocladus*, it has been found only in *Gleditsia* (Lee, unpublished data) and subg. *Guilandina* of *Caesalpinia* (Gillis & Proctor, 1974). All three of these genera belong to the tribe Caesalpinieae.

originated in monsoon countries with warm subtropical climates, i.e., in southern Yunnan and the adjacent areas of Tonkin and Assam. Although more information is needed to substantiate Takhtajan's hypothesis, recent works on the affinities of the Chinese tropical zone (Wu, 1965) and extensive floristic studies in southern Yunnan (Wu & Wang, 1957-1958; Wu & Li, 1965) indicate a high concentration of ancient tropical floristic elements in these areas.

On the basis of an extensive study of the tropical and subtropical flora of southern and southeastern Yunnan, Wu and Wang (1957-1958) proposed three possible migrational routes of the ancient (Tertiary) tropical flora of the southeastern Yunnan-Tonkin region. These are route 1: via Vietnam, Borneo, and the Philippines to Taiwan; route 2: via Kwangsi and Kwangtung to Hainan; and route 3: via Kweichow, Hopeh, and Szechwan to Kiangsu and Chekiang, and extending westward to the border of the Szechwan-Shikong highlands, with the northwestern boundary in Tsin-ling and Huai-ho. These routes, particularly "route 3," may be responsible for the "tropical floristic elements" presently found in the temperate regions of China.

Morphologically, particularly in foliar characteristics, the Asiatic species of *Gymnocladus* form a coherent group, which differs from its counterpart in eastern North America. Thus it is reasonable to assume that the separation of the two groups took place quite early. In addition, the presence of two upland species in eastern Asia may be explained by the gradual, rather recent orogenesis and the relatively stable climate in the southwestern border area of China. These conditions seem to provide a more favorable environment for conserving a greater number of species than those in eastern North America.

With the exception of its being dioecious, the genus *Gymnocladus* possesses several presumably primitive characteristics: its flowers are relatively undifferentiated, with five or four subequal calyx lobes and the same number of petals; its fruits dehisce along the adaxial (placental) suture, resembling a follicle; its seeds have copious endosperm; and its leaves have a subopposite to opposite arrangement of leaflets. All of these characteristics suggest that the genus represents a relatively primitive group within the Caesalpinioideae. Hence the association of dioecism with such a group may serve as indirect evidence for the early occurrence of this derived character.

TAXONOMIC TREATMENT

Gymnocladus Lamarck, Encycl. Méth. Bot. 1: 733 (in part). 1785;
Tableau Encycl. Méth. II. 5(1): pl. 823. 1793; *Ibid.* III. 412. 1796.

Guilandina L. Sp. Pl. 381 (in part). 1753.

Hyperanthera Vahl, Symb. Bot. 1: 30 (in part). 1790.

Unarmed trees. Leaves deciduous, bipinnate, the stipules lanceolate to obovate, or absent; leaflets obovate, oblong to narrowly oblanceolate,

the two stipels small, awl-shaped and persistent, or absent. Inflorescence racemose to paniculate, terminal or axillary. Flowers regular, predominantly dioecious to polygamous, pedicellate, the bracts and bracteoles minute, pointed, deciduous or not; calyx tubular, ridged, 5-lobed; petals 5 or 4, creamy white or purplish; stamens 10, inserted on the calyx tube, with fertile anthers or not; ovary sessile, 4- to many-ovuled, rudimentary or absent in the staminate flowers. Fruit oblong to falcate, turgid to compressed, woody, pulpy inside, 1- to several-seeded, dehiscent along the placental suture. Seeds ovoid to subglobose, with stout funicles and thick, bony, dark brown testa; endosperm present.

TYPE SPECIES: *Gymnocladus canadensis* Lam. = *G. dioicus* (L.) K. Koch.

The original description of the genus includes both *Gymnocladus canadensis* and *G. arabica*, but later exclusion of *G. arabica* leaves *G. canadensis* (*G. dioicus*) as the type of the genus.

KEY TO THE SPECIES OF GYMNOCLADUS

1. Mature leaflets ovate, acuminate; widest part of leaflets exceeding 2 cm.; stipels absent (North American species). *G. dioicus*.
1. Mature leaflets oblong to oblanceolate, rarely lanceolate, obtuse to slightly retuse, occasionally acute; widest part of leaflets never exceeding 2 cm.; stipels small, awl-shaped, and persistent (Asiatic species).
 2. Leaflets oblanceolate to lanceolate, acute to pointed; pinnae usually in 3 pairs. *G. burmanicus*.
 2. Leaflets oblong, obtuse to slightly retuse; pinnae in 3-7 pairs.
 3. Fruit falcate, the pericarp with apparent ridges and grooves showing seeds within. *G. assamicus*.
 3. Fruit oblong to subfalcate, the pericarp more or less smooth. *G. chinensis*.

Gymnocladus dioicus (L.) K. Koch, Dendrology 1: 5. 1869.

FIGURE 2.

Guilandina dioica L. Sp. Pl. 381. 1753.

Gymnocladus canadensis Lam. Encycl. Méth. Bot. 1: 733. 1785; Tableau Encycl. Méth. II. 5(1): pl. 823. 1793; *Ibid.* III. 412. 1796.

Hyperanthera dioicus (L.) Vahl, Symb. Bot. 1: 31. 1790.

Trees 10-30 m. tall, the bark deeply fissured, dark gray throughout or tinged with red, 2 to 3 cm. thick. The rachis of the leaves 60-90 cm. long, glabrate or tomentose, with 5 to 7 pairs of pinnae 15-25 cm. long; pinnae 4-7-jugate, the lower pairs with single leaflets; leaflets ovate, 5-6.5 × 2.5 cm., or those replacing the lowest or occasionally the 2 lower pairs of pinnae sometimes twice as large, glabrate on both surfaces, with the exception of a few scattered hairs along the midrib, the apex short-acuminate, the base cuneate or rounded, slightly oblique, stipels absent. Inflorescence of the staminate flower 7.5-10 cm. long; inflores-

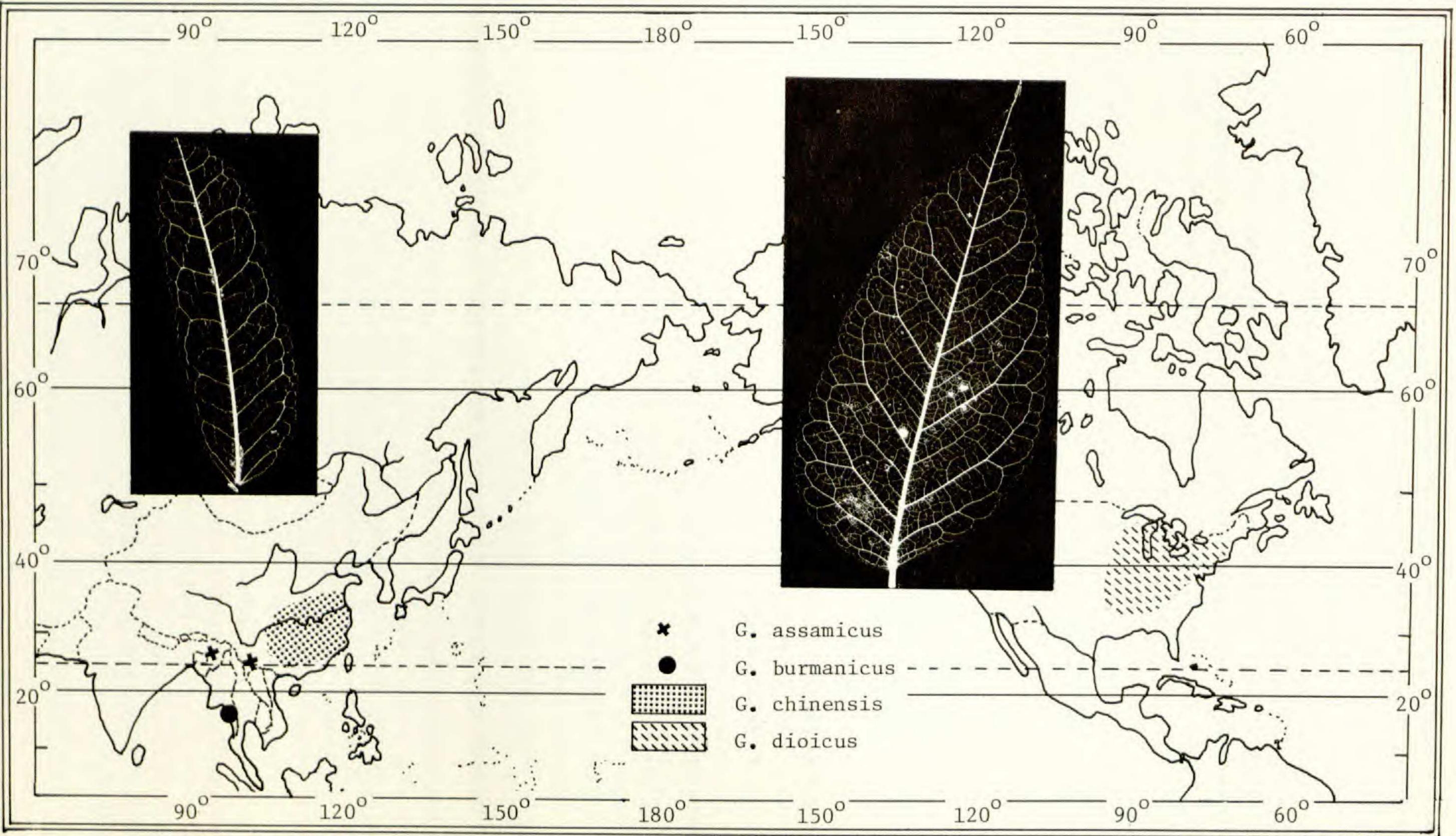


FIGURE 2. Distribution of the genus *Gymnocladus*. Inserts showing venations of *G. chinensis* (left) and *G. dioicus* (right).

cence of the carpellate ("perfect") flower 25–30 cm. long, the branches hoary-tomentose. Flowers on stout pedicels 1.5–2 cm. long or longer in the staminate flowers, with strong fragrance; calyx tube 6–12 mm. long, the lobes 5–4, lanceolate, 4–6 mm. long; petals 5–4, 5–7 mm. long, 1.5–2.5 mm. wide, slightly keeled, pilose on the back, tomentose on the inner surface, greenish white; stamens ca. 5 mm. long, the anthers orange to yellowish, fertile or abortive; ovary with scattered whitish pilosity, elongate, with 2–8 ovules, rudimentary or absent in the staminate flowers, the stigma slightly bilobed, acuminate at the apex. Fruit oblong to slightly falcate, 15–25 cm. long, 3.5–5 cm. wide, and 1–2 cm. thick, dark brown, covered with a glaucous bloom, on a stout stalk 2.5–5 cm. long, pulpy inside (the pulp greenish when fresh, turning yellow to brownish in age). Seeds 1–6, ca. 1.5–2 cm. long, 1.5–2 cm. wide, and 0.6–0.8 cm. thick. Chromosome number $2n = 28$.

TYPE. In the protologue of *Guilandina dioica* (Linnaeus, 1753), the only reference to earlier literature is that to the second edition of the *Genera Plantarum* (Linnaeus, 1742). In this earlier reference Linnaeus mentioned that he had seen male plants of this species growing in Paris and that fruits were common in museums. There is no material referable to *Guilandina dioica* in Linnaeus's herbarium, but it is possible that fruiting material which he saw is still extant. Hence *Gymnocladus dioicus* may be typified, at least for the time being, by Linnaeus's description in the second edition of *Genera Plantarum* (1742, p. 518).

The name *Gymnocladus canadensis*, on the other hand, is superfluous, since Lamarck referred to *Guilandina dioica* L.

HABITAT AND DISTRIBUTION. This bottomland species is found from central New York and Pennsylvania west through southern Ontario and southern Michigan to the valley of the Minnesota River, eastern Nebraska, Kansas, and western Oklahoma, and south between the Mississippi River and the Allegheny Mountains to Tennessee (Pinchot, 1907).

VERNACULAR NAMES. Kentucky coffee-tree (U.S.) and chicot (Canada).

REPRESENTATIVE SPECIMENS. U.S.A. ALABAMA: northeast of Sheffield, Colbert Co., Oct. 7, 1934, *Harper 3273* (GH). ARKANSAS: Cotter, Marion Co., Sept. 1, 1915, *Palmer 8406* (A); Shirley, Van Buren Co., May 28, 1924, *Palmer 25204* (A). ILLINOIS: near Shawneetown, Gallatin Co., June 6, 1919, *Palmer 15522* (A); Alto Pass, Union Co., May 3, 1919, *Palmer 15037* (A). IOWA: near Burlington, Des Moines Co., Sept. 5, 1921, *Palmer 20331* (A); Sidney, July 12, 1925, *Pammel 414* (GH). KANSAS: near Neodesha, Wilson Co., May 5, 1922, *Palmer 21140* (A); Riley Co., Oct. 2, 1895, *Norton 124a* (GH). KENTUCKY: Mt. Sterling, Montgomery Co., May 24, 1926, *Horsey 2313* (A); Richmond, Madison Co., May 15, 1920, *Horsey 1064* (A). MARYLAND: Baltimore Co., Sept. 1980, *Taylor s.n.* (GH). MICHIGAN: Hubbardston, Ionia Co., Sept. 6, 1890, *Wheeler s.n.* (A). MISSOURI: near Forest City, Holt Co., June 12, 1924, *Palmer 25401* (A); Red Oak, Lawrence Co., May 1, 1925, *Palmer 26977* (A). NEW YORK: Syracuse, Oct. 6, 1935, *Brown 8009A* (A); Tompkins Co., July 19, 1915, *MacDaniels 4395* (GH). NORTH CAROLINA: Mecklenburg Co., May

13, 1968, *Matthews et al. s.n.* (GH). OHIO: near Cincinnati, May 27, 1890, *Lloyd s.n.* (GH); Buena Vista, Sept. 14, 1936, *M. C. Smith 8242* (A). OKLAHOMA: Canton, Aug. 16, 1915, *Andrews 56* (A); near Tonkawa, Kay Co., Aug. 4, 1913, *Stevens 1829* (A). TENNESSEE: near Nashville, May, 1880, *Gattinger s.n.* (A); near Pegram, Cheatham Co., April 24, 1929, *Palmer 35508* (A). VIRGINIA: northwest of Return, Oct. 15, 1941, *Fernald & Long 13956* (GH). WEST VIRGINIA: Dickson, Wayne Co., July 20, 1936, *Gilbert 494* (GH). WISCONSIN: west of Milwaukee, Oct. 3, 1918, *Slavin 476* (A); south of Oshkosh, Winnebago Co., July 19, 1934, *Fassett & Truman 16869* (GH). Canada. ONTARIO: Norfolk Co., June 25, 1941, *Soper 2636* (GH); Lambton Co., Aug. 11, 1941, *Soper 2831* (GH); Pelee Island, July 28, 1892, *Macoun s.n.* (GH).

Although distributed over a wide area, *Gymnocladus dioicus* is one of the rarest of the forest trees of eastern North America (Sargent, 1892). It occurs usually as a single tree or in small clusters in localities most favorable to its growth. Over large areas within its range it is entirely lacking or represented only by an occasional individual (Pinchot, 1907). The range of this species is suspected by some to be associated with Indian camp sites or with the lands of the early settlers (Robert Bye, pers. comm.). Pinchot, however, indicates that the economic planting range of this species coincides with the natural range and may in places be extended beyond it.

The tree is often cultivated for ornamental purposes. The fruits, preserved like those of the tamarind, are said to be wholesome and slightly aperient (Hedrick, 1919). It should be cautioned that although the pod and particularly the pulpy tissue, which are rich in saponins, may be harmless when taken internally, painful death would result if an aqueous extraction of the fruit were injected intravenously, since the saponin in the solution lysolizes the red blood cells even in an extremely low concentration. Roasted seeds of *Gymnocladus dioicus* were employed by the early settlers of Kentucky as a substitute for coffee (Browne, 1846).

Gymnocladus chinensis Baillon, Compt. Rend. Assoc. Franç. Avanc. Sci. 3: 418-427. t. 4. 1875. FIGURE 2.

Trees 5-12 m. tall, the bark gray, usually smooth. The rachis of the leaves 25-30 cm. long, shortly and sparsely pubescent to glabrate, with 3-5 pairs of pinnae 14-28 cm. long; pinnae 10- to 12-jugate; leaflets oblong to elongate-oblong, 1.5-4 × 1-1.5 cm., densely whitish-tomentose on both sides when young, becoming glabrate with age, the apex rounded or slightly retuse, the stipels 1, ca. 1 mm. long, awl-shaped, and persistent. Inflorescence 4-10 cm. long, hoary-tomentose. Flowers with pedicel 1-2 cm. long, erect or pendulous; calyx tube 5-6 mm. long, the lobes lanceolate, ca. 4 mm. long, 2 mm. wide; petals oblong, ca. 5 mm. long, 2 mm. wide, lilac-purple; stamens ca. 4 mm. long, pilose near the base; ovary elongate, glabrate, usually 4-ovulate, rudimentary or absent in the staminate flowers, the style short, the stigma recurved-capitate. Fruit oblong, 7-12 cm. long, 3-4 cm. wide, and ca. 1.5 cm. thick, shortly

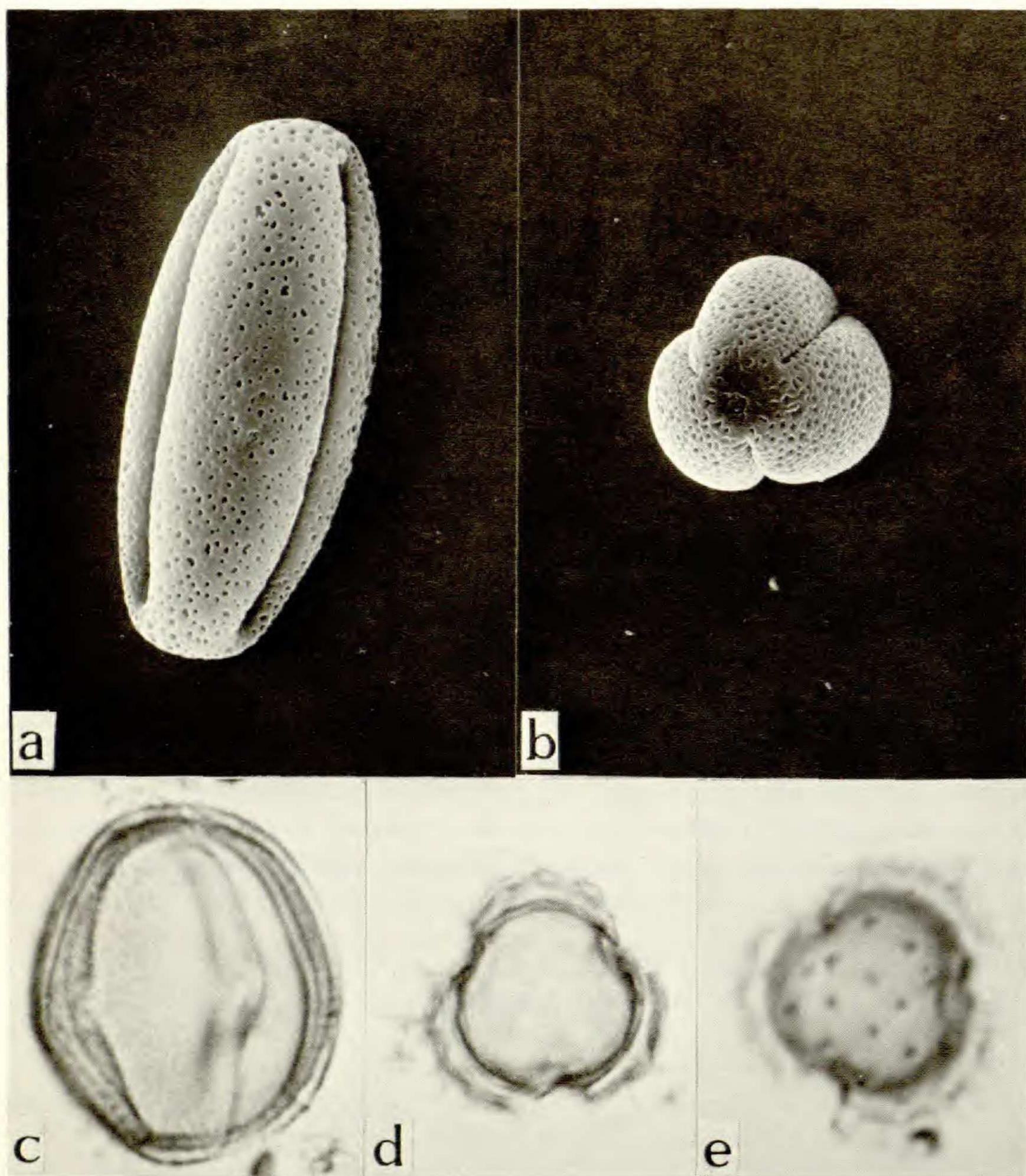


FIGURE 3. Pollen grains of *Gymnocladus dioicus*: a & b, SEM micrographs, pollen untreated, ca. $\times 1400$; c-e, light microscope micrographs, pollen aceto-lized, ca. $\times 1000$.

beaked, dark brown, usually covered with a glaucous bloom. Seeds 2-4, subglobose to ovoid, 1.5-2 cm. long, 1.5-1.8 cm. wide, and 1-1.2 cm. thick.

TYPE. Since no specimen of *Gymnocladus chinensis* is known in existence in the Baillon Herbarium, Laboratoire de Phanérogamie, Paris, the figure that appeared in the original article (Compt. Rend. Assoc. Franç. Avanc. Sci. 3: 418-427. t. 4. 1875) is designated here as the type of the species.

HABITAT AND DISTRIBUTION. *Gymnocladus chinensis* is the most widely distributed species of the genus. It has been reported in central and southeastern China, in the provinces of Anhwei, Chekiang, Fukien, Hunan, Hupeh, Kiangsi, Kwangtung, and Szechwan.

VERNACULAR NAMES. Fe-tsaou-tow and yu-tsao-chio (China).

REPRESENTATIVE SPECIMENS. China. ANHWEI: Chiu Hwa Shan, Aug. 21, 1934, *Fan & Li* 284 (A, E); Huang Shan, Jan. 11, 1964, *H. Chiu* 163 (PE). CHEKIANG: Howchow, Oct. 12, 1928, *Chiao* 18894 (A, US); region 20 to 40 miles west of Wenchow, June 6-8, 1924, *Ching* 1891 (A); between Ping Yung and Tai Suan, July 20, 1924, *Ching* 2174 (A). FUKIEN: Yenping, June 20, 1925, *Ching* 3480 (A). HUNAN: Yi Chang Hsien, May 1-13, 1934, *Tsang* 23793 (US). HUPEH: Oct. 1887, *Henry* 2873 (A, K), *Henry* 5576a (A); Nan-T'o and mountains to northward, *Henry* 3873 (A, K); western Hupeh, Patung, May 1907, *Wilson* 760 (A); Hsing-Shan Hsien, May 6, 1907, *Wilson* 760 (A), Dec. 1907, *Wilson* 760 (A), and other specimens labeled *Wilson* 760 with various localities and dates in A, E, K, NY, and US. KIANGSI: Kiukiang, Aug. 1909, *Wilson* 1598 (A, E). KWANGTUNG: Tsung-fa Hsien, Sam Kok Shan, May 1-25, 1935, *Tsang* 25144. SZECHWAN: 1885-1888, *Henry* 5576 (E, US); Omei Hsien, Mt. Omei, 1891, *Feber s.n.* (LE); Aug. 25, 1928, *Fang* 3342 (A, P, PE).

The fruit of *Gymnocladus chinensis* is highly esteemed for its saponaceous qualities and is much desired as a soap substitute in China. It is also used as an herb medicine in curing swellings and abscesses. Oil from seeds is used as latex in making paints.

Gymnocladus chinensis and the rest of the Asiatic species form a coherent group within the genus, and they may be easily separated from the American species, *G. dioicus*, by their much narrower leaflets, which rarely exceed 2 cm., and by the presence of small awl-shaped and persistent stipels.

Gymnocladus assamicus U. N. Kanjilal ex P. C. Kanjilal, Assam Forests Rec. Bot. 1: 7, 8. 1934. FIGURE 4.

Trees 5-17 m. tall, the bark yellowish to reddish brown, reticulate. The rachis of the leaves 30-40 cm. long, glabrate to obscurely glandular, with 6-7 pairs of pinnae 11-22.5 cm. long; pinnae 12-14-jugate; leaflets oblong to obovate-oblong, 2-3 × 0.6-1.5 cm., glabrate above, minutely pubescent beneath on the midrib, the apex rounded to obtusely mucronate, the base rounded to cuneate, slightly oblique, the stipel 1, ca. 1 mm. long, awl-shaped, and persistent. Inflorescence racemose, 11-17 cm. long, densely gray, densely pubescent, the bracts and bracteoles minute or absent. Flowers pedicellate, the pedicels ca. 4 mm. long; calyx tube 6-9 mm. long, villous outside, 5-lobed, the lobes 4-6 mm. long, lanceolate to subulate; petals 5, oblong-obovate, 7-9 mm. long, purplish gray; stamens with densely pilose filaments ca. 3 mm. long, the anthers oblong-ovoid; pistil not seen. Fruit oblong, subfalcate, compressed, 14-18 cm. long, 3-4 cm. wide, and 1.5 cm. thick, shortly beaked, with a stalk ca. 8 mm. long, reddish brown, pulp present, the pericarp rather thick, woody,

transversely ridged and grooved (showing the seeds within). Seeds 6–8, obovoid to subglobose, bluntly trigonous, 1.5–2.0 cm. long, 1.2–1.6 cm. wide, with funicles ca. 8 mm. long.

TYPE. India, Assam. Khasi Hills, Laitkseh, 1800 m., *Shillong Herb. no. 7624* (Isotype, SH).

HABITAT AND DISTRIBUTION. This species has hitherto been known only from the type locality in Assam, India. Recent study of Chinese caesalpiniaceous plants, however, shows that a specimen collected in southeastern Yunnan also belongs to this species, suggesting a wider distribution than previously indicated.

ADDITIONAL SPECIMENS. India. ASSAM: Khasi Hill, *Shillong Herb. nos. 10157 and 10548* (not seen by the writer). China. SE YUNNAN: Mar-li-po, Village of Chung-dzai, in an open "thicket" at the elevation of 1800–1900 m., Nov. 4, 1947, *Feng 12863* (A).

Gymnocladus assamicus is closely related to other Asiatic species of the genus. It is characterized by its more or less falcate fruit, which is transversely ridged and grooved on the surface.

The Khasis use the fleshy pods as a soap substitute for washing their hair.

Gymnocladus burmanicus C. E. Parkinson, Bull. Misc. Inf. Kew 1928: 333. 1928. FIGURE 4.

Trees ca. 17 m. tall, the bark brown with transverse lines. The rachis of the leaves ca. 20 cm. long, shortly and sparsely pubescent to glabrate, usually with 3 pairs of pinnae 8–15 cm. long; pinnae 7–10-jugate; leaflets 4–6 cm. long, 0.5–1.5 cm. wide, the lower ones ovate-lanceolate and oblique, the upper ones lanceolate or nearly so, their bases narrowed, the apex of all leaflets acute to acuminate, with scattered, short, appressed trichomes when young, becoming glabrate in age, the petiolules ca. 2 mm. long, the stipel 1, 1–2 mm. long, awl-shaped, and persistent. Inflorescence ca. 10 cm. long, all the branches shortly and sparsely pubescent. Flowers with pedicel 1–1.3 cm. long; calyx tube ca. 7 mm. long, 5-lobed, the lobes ca. 5 mm. long; petals 5, oblong, pale-pubescent, 8 mm. long, reddish purple; stamens with filaments ca. 7 mm. long, the anthers ovoid; ovary glabrous, few-ovuled, the style short, the stigma slightly oblique. Fruit oblong, subcylindrical, slightly compressed, ca. 8 cm. long, 3 cm. wide, reddish brown, shiny, pulp present. Seeds 2 to 3, oblong-obovoid.

TYPE. Lower Burma, Ta-ok Plateau, Dawna Hill of Tenasserim, at about 1000 m., *Parkinson 5229* (K).

HABITAT AND DISTRIBUTION. This species is known solely from the type collection. According to A. Das (see Kanjilal, 1934), the range of this species extends to adjacent India (Assam); however, no specimen has been recorded from that area.

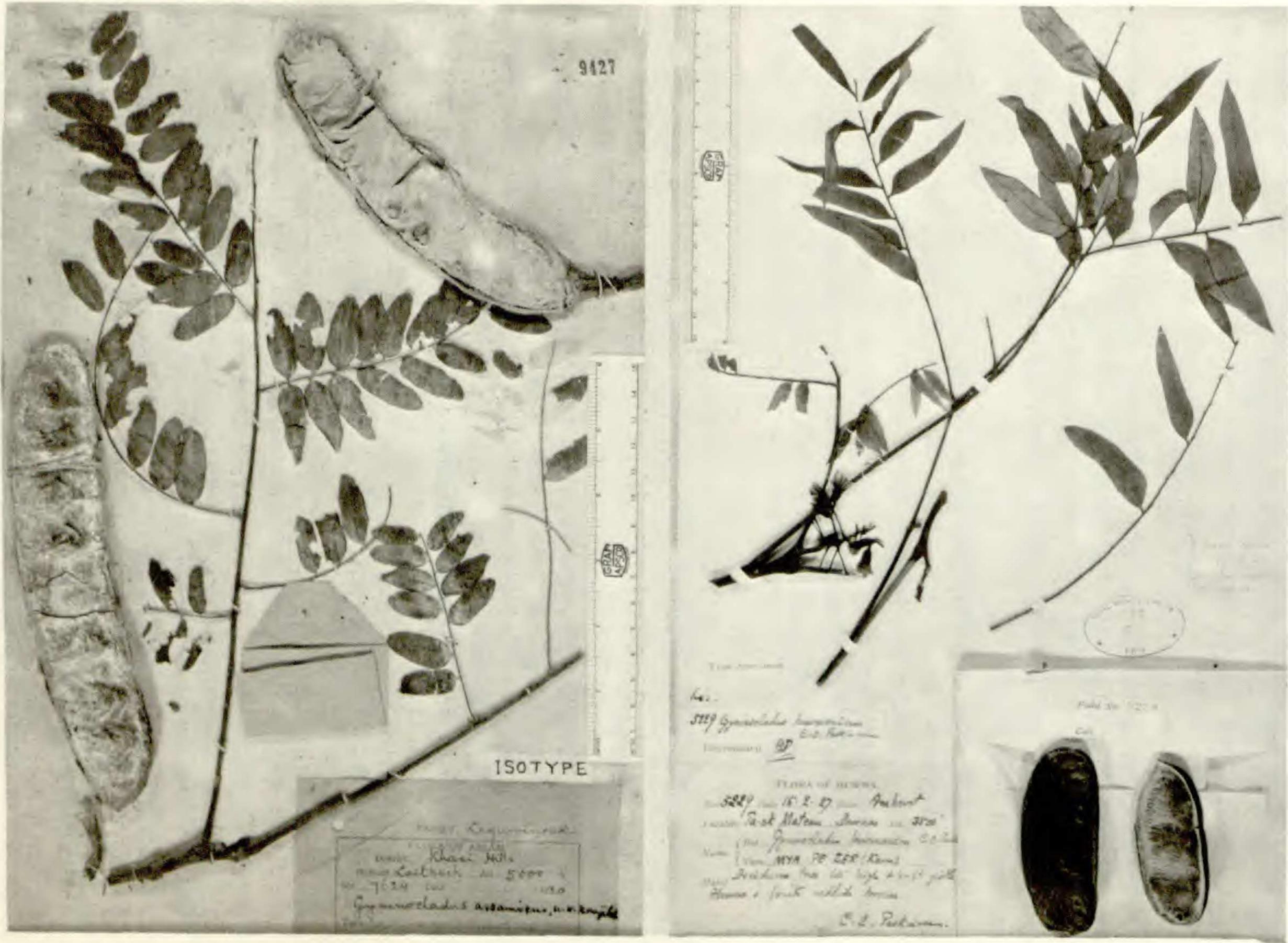


FIGURE 4. Types of *Gymnocladus assamica* (left) and *G. burmanicus* (right).

VERNACULAR NAME. Mya-pe-ler (Karen, Lower Burma).

Gymnocladus burmanicus may be separated from other Asiatic species by the narrower, ovate-lanceolate leaflets; the usually larger and reddish purple flowers; and the reddish brown, subcylindrical fruits.

ACKNOWLEDGMENTS

I would like to thank Dr. R. A. Howard, Director, and other staff members of the Arnold Arboretum for their cooperation and assistance during my tenure as a Mercer Fellow of the Arboretum. Special recognition is due to Dr. B. G. Schubert for her constant advice and guidance throughout this study.

I also appreciate the chemical data provided by Dr. R. M. Parkhurst, Stanford Research Institute, Menlo Park, California. My gratitude is expressed to the curators of the herbaria listed in the text for loaned material essential to this study. Grateful acknowledgment is made for the Martha Dana Mercer Trust funds granted to me through the Arnold Arboretum during the academic years of 1973 and 1974.

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